Reprinted from the American Journal of Physiology.

Vol. XXIX. — March 1, 1912. — No. V.

AN EXPLANATION OF HUNGER.

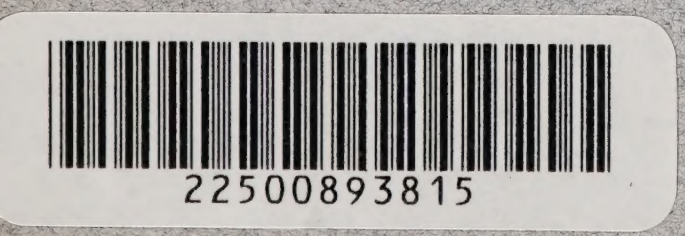
By W. B. CANNON and A. L. WASHBURN.

[From the Laboratory of Physiology in the Harvard Medical School.]

UNIVERSITY COLLEGE LONDON.
CANCELLED

£.

WELLCOME INSTITUTE
LIBRARY
Coll. WI
Coll. num.
No. WI 100
1912
C22e



Reprinted from the American Journal of Physiology.
Vol. XXIX. — March 1, 1912. — No. V.

AN EXPLANATION OF HUNGER.[1]

By W. B. CANNON and A. L. WASHBURN.

[*From the Laboratory of Physiology in the Harvard Medical School.*]

HUNGER and appetite are so intimately interrelated that a discussion of either requires each to be clearly defined. According to one view the two experiences differ only quantitatively, appetite being a mild stage of hunger.[2] Another view, better supported by observations, is that the two experiences are fundamentally different.[3]

Appetite is related to previous sensations of the taste and smell of food; it has therefore, as Pawlow has shown, important psychic elements. It may exist separate from hunger, as, for example, when we eat delectable dainties merely to please the palate. Sensory associations, delightful or disgusting, determine the appetite for any edible substance, and either memory or present stimulation can thus arouse desire or dislike for food.

Hunger, on the other hand, is a dull ache or gnawing sensation referred to the lower mid-chest region and the epigastrium. It is the organism's first strong demand for nutriment, and, not satisfied, is likely to grow into a highly uncomfortable pang, less definitely localized as it becomes more intense. It may exist separate from appetite, as, for example, when hunger forces the taking of food not only distasteful but even nauseating. Besides the dull ache, however, lassi-

[1] The indicative evidence of the results here reported was presented to the Boston Society of Medical Sciences, January 17, 1911. See Cannon: The mechanical factors of digestion, London and New York, 1911, p. 204. The full account was presented to the Harvey Society, New York City, December 16, 1911.

[2] Bardier: Richet's Dictionnaire de physiologie, article "Faim," 1904, vi, p. 1; Howell: Text-book of physiology, fourth edition, Philadelphia and London, 1911, p. 285.

[3] See Sternberg: Zentralblatt für Physiologie, 1909, xxii, p. 653. Similar views were expressed by Bayle in a thesis presented to the Faculty of Medicine in Paris in 1816.

tude and drowsiness may appear, or faintness, or headache, or irritability and restlessness such that continuous effort in ordinary affairs becomes increasingly difficult. That these states differ with individuals — headache in one, faintness in another, for example — indicates that they do not constitute the central fact of hunger, but are more or less inconstant accompaniments, for the present negligible. The dull, pressing sensation is the constant characteristic, the central fact, to be examined in detail.

Of the two theories of hunger — (1) that it is a general sensation with a local reference, and (2) that it has a local peripheral source — the former has been more widely accepted. The support for that theory can be shown to be not substantial. The wide acceptance of the theory, however, warrants an examination of it in some detail.

Hunger not a General Sensation.

Underlying the idea that hunger arises from a general condition of the body is the consideration that, as time passes, food substances disappear from the blood, and consequently the nerve cells, suffering from the shortage of provisions, give rise to the sensation.[4]

In support of this view the increase of hunger as time passes has been pointed out. There is abundant evidence, however, that the period of increase is short, and that during continued fasting hunger wholly disappears after the first few days.[5] On the theory that hunger is a manifestation of bodily need, we must suppose that the body is mysteriously not in need after the third day, and that therefore hunger disappears. The absurdity of such a view is obvious.

Continued hunger soon after eating (when the stomach is full), especially in cases of duodenal fistula,[6] and satisfaction when the escaping chyme is restored to the intestine, have been cited as ruling

[4] Schiff: Physiologie de la digestion, Florence and Turin, 1867, p. 40.

[5] See Luciani: Das Hungern, Hamburg and Leipzig, 1890, p. 113; Tigerstedt: Nagel's Handbuch der Physiologie, Berlin, 1909, i, p. 376; Johansson, Landergren, Sondén, and Tigerstedt: Skandinavisches Archiv für Physiologie, 1897, vii, p. 33; Carrington: Vitality, fasting and nutrition, New York, 1908, p. 555; Viterbi: quoted by Bardier, *Loc. cit.*, p. 7.

[6] See Busch: Archiv für pathologische Anatomie und Physiologie und für klinische Medicin 1858 xiv p 147.

out the peripheral and thus favoring the central origin of the sensation. As will be seen later, however, other possible peripheral sources of hunger exist besides the stomach. Further consideration of this point will be given in due course.

Because animals eat, sometimes eagerly, when the gastro-intestinal tract is wholly separated from the central nervous system,[7] the conclusion has been drawn that hunger must be a general sensation and not of peripheral origin. But appetite as well as hunger may lead to eating. As Ludwig stated many years ago, even if all afferent nerves were severed, psychic reasons still could be given for the taking of food.[8] Indeed, who accepts dessert because he is hungry? Evidently, since hunger is not required for eating, the fact that an animal eats is no testimony whatever that the animal is hungry, and therefore, after nerves have been severed, is no proof that hunger is of central origin.

Further objections to the theory that hunger is a general sensation lie in the weakness of its main assumption and in its failure to account for certain well-known observations. Thus no evidence exists that the blood has in fact changed when hunger appears. Moreover in fever, when bodily stores are being most rapidly destroyed, and when therefore, according to this theory, hunger should be most insistent, the sensation is wholly absent. And the quick abolition of the pangs soon after food is taken, before digestion and absorption can have proceeded far, as well as the quieting effect of swallowing indigestible stuff, such as moss and clay, further weakens the argument that the sensation arises directly from lack of nutriment in the body.

Many have noted that hunger has a sharp onset. If this abrupt arrival of the characteristic ache corresponds to the general bodily state, the change in general bodily state must occur with like suddenness, or have a critical point at which the sensation is instantly precipitated. No evidence exists that either of these conditions occurs in metabolism.

Another peculiarity of hunger which we have noticed is its intermittency. It may come and go several times in the course of a few hours. Furthermore, during a given period, the sensation is not

[7] See SCHIFF: *Loc. cit.*, p. 37; also DUCCESCHI: Archivio di fisiologia, 1910, viii, p. 582.

[8] LUDWIG: Lehrbuch der Physiologie des Menschen, Leipzig and Heidelberg, 1858, ii, p. 584.

uniform in intensity, but is marked by ups and downs, sometimes changing to alternate presence and absence without alteration of rate. Our observations have been confirmed by psychologists, trained to introspection, who have reported that the sensation has a distinctly intermittent course.[9] In the experience of one of us (C.) the hunger pangs came and went on one occasion as follows:

Came	Went
12–37–20	12–38–30
40–45	41–10
41–45	42–25
43–20	43–35
44–40	45–55
46–15	46–30

and so on, for ten minutes longer. Again in this relation, the intermittent and periodic character of hunger would require, on the central theory, that the bodily supplies be intermittently and periodically insufficient. During one moment absence of hunger would imply abundance of nutriment in the organism, ten seconds later presence of hunger would imply that the stores had been suddenly reduced, ten seconds later still absence of hunger would imply sudden renewal of plenty. Such zigzag shifts of the general bodily state may not be impossible, but, from all that is known of the course of metabolism, they are highly improbable. The periodicity of hunger, therefore, is further evidence against the theory that the sensation has a general basis in the body.

The last objection to this theory is its failure to account for the most common feature of hunger, — the reference of the sensation to the epigastric region. Schiff and others[10] have met this objection by two contentions. First, they have pointed out that hunger is not always referred to the stomach. Schiff interrogated ignorant soldiers regarding the local reference; several indicated the neck or chest, twenty-three the sternum, four were uncertain of any region, and two only designated the stomach. In other words, the stomach region was most rarely mentioned.

[9] We are indebted to Prof. J. W. Baird of Clark University, and his collaborators, for this corroborative testimony.

[10] See Schiff: *Loc. cit.*, p. 31; Bardier: *Loc. cit.*, p. 16.

The second contention against the importance of local reference is that such evidence is fallacious. Just as the reference of tinglings to fingers which have been removed from the body does not prove that the tinglings originate in those fingers, so the assignment of the ache of hunger to any special region does not demonstrate that the ache arises from that region.

Concerning these arguments we may recall first Schiff's admission that the soldiers he questioned were too few to give conclusive evidence. Further, the testimony of most of them that hunger seemed to originate in the region of the sternum cannot be claimed as unfavorable to a peripheral source of the sensation. The description of feelings which develop from disturbances within the body is almost always indefinite; the testimony is not, therefore, dismissed as worthless. On the contrary, such testimony is used constantly in judging internal disorders.

The force of the contention that reference to the periphery is not proof of the peripheral origin of a sensation depends on the amount of accessory evidence which is available. Thus, if an object is seen coming into contact with a finger, the simultaneous sensation of touch referred to that finger may reasonably be assumed to have resulted from the contact, and not to have been a purely central experience accidentally attributed to an outlying member. Similarly in the case of hunger — all that is needed as support for the peripheral reference of the sensation is proof that conditions occur there, simultaneously with hunger pangs, which might reasonably be regarded as giving rise to those pangs. In the fasting stomach may not conditions, in fact, be present which would sustain the theory that hunger has a local peripheral source?

Certain assumptions have been made regarding the state of the fasting stomach, and certain inferences have been drawn from these assumptions which must be considered before the results we have to present will have a proper setting.

Objections to some Theories that Hunger is of Local Origin.

Hunger is not due to emptiness of the stomach, for Nicolai found after gastric lavage that the sensation did not appear in some instances

for more than three hours.[11] This testimony confirms Beaumont's observation on Alexis St. Martin, that hunger arises some time after the stomach is evacuated.[12]

Hunger is not due to hydrochloric acid secreted into the empty stomach. The gastric wash-water from hungry subjects is neutral or only slightly acid.[13] Furthermore, persons suffering from achylia gastrica declare that they have normal feelings of hunger.

Hunger is not due to turgescence of the gastric glands. This theory, propounded by Beaumont,[14] has commended itself to several recent writers. Thus Luciani has accepted it, and by adding the idea that nerves distributed to the mucosa are specially sensitive to deprivation of food, he accounts for the hunger pangs.[15] Also Valenti declared two years ago that the turgescence theory of Beaumont is the only one possessing a semblance of truth.[16] The experimental work reported by these two investigators, however, does not necessarily support the turgescence theory. Luciani severed in fasting dogs the previously exposed and cocainized vagi, and Valenti merely cocainized the nerves; the dogs, eager to eat a few minutes previous to this operation, now ran about as before, but when offered food, licked and smelled it, but did not take it. This total neglect of the food lasted varying periods up to two hours. The vagus nerves seem, indeed, to convey impulses which affect the procedure of eating, but there is no clear evidence that those impulses arise from distention of the gland cells. The turgescence theory would also meet difficulties in an attempt to explain the disappearance of hunger after the swallowing of indigestible material; for such material, not being appetizing, does not cause any secretion of gastric juice.[17] Furthermore, Nicolai found that the sensation could be abolished by simply introducing a stomach tube. The turgescence of the gastric glands would not be

[11] Nicolai: Ueber die Entstehung des Hungergefühls, Inaugural-Dissertation, Berlin, 1892, p. 17.

[12] Beaumont: The physiology of digestion, second edition, Burlington, 1847, p. 51.

[13] Nicolai: *Loc. cit.*, p. 15.

[14] Beaumont: *Loc. cit.*, p. 55.

[15] Luciani: Archivio di fisiologia, 1906, iii, p. 542.

[16] Valenti: Archives italiennes de biologie, 1910, liii, p. 97.

[17] See Pawlow: The work of the digestive glands, London, 1902, p. 70; Hornborg: Skandinavisches Archiv für Physiologie, 1904, xv, p. 248.

reduced by either of these procedures. The turgescence theory, finally, does not explain the quick onset of hunger, or its intermittent and periodic character, for the cells cannot be repeatedly swollen and contracted within periods a few seconds in duration.

Hunger the Result of Contractions.

There remain to be considered, as a possible cause of hunger pangs, contractions of the stomach and other parts of the alimentary canal. This suggestion is not new. Sixty-six years ago Weber declared his belief that "strong contraction of the muscle fibres of the wholly empty stomach, whereby its cavity disappears, makes a part of the sensation which we call hunger." [18] Vierordt drew the same inference twenty-five years later (in 1871); [19] and since then Knapp and also Hertz have declared their adherence to this view. These writers have not brought forward any direct evidence for their conclusion, though Hertz has cited Boldireff's observations on fasting dogs as probably accounting for what he terms "the gastric constituent of the sensation." [20]

The argument commonly used against the contraction theory is that the stomach is not energetically active when empty. Thus Schiff stated "the movements of the empty stomach are rare and much less energetic than during digestion." [21] Luciani expressed his disbelief by asserting that gastric movements are much more active during gastric digestion than at other times, and cease almost entirely when the stomach has discharged its contents.[22] And Valenti stated only year before last: "We know very well that gastric movements are exaggerated while digestion is proceeding in the stomach, but when the organ is empty they are more rare and much less pronounced," and therefore they cannot account for hunger.[23]

Contractions of the alimentary canal in fasting animals. — Evidence opposed to these suppositions has been in existence for many years.

[18] Weber: Wagner's Handwörterbuch der Physiologie, 1846, iii [2], p. 580.

[19] Vierordt: Grundriss der Physiologie, Tübingen, 1871, p. 433.

[20] Knapp: American medicine, 1905, x, p. 358; Hertz: The sensibility of the alimentary canal, London, 1911, p. 37.

[21] Schiff: *Loc. cit.*, p. 33.

[22] Luciani: *Loc. cit.*, p. 542.

[23] Valenti: *Loc. cit.*, p. 97.

In 1899 Bettmann called attention to the contracted condition of the stomach after several days' fast.[24] In 1902 Wolff reported that after forty-eight hours without food the stomach of the cat may be so small as to look like a slightly enlarged duodenum.[25] The anatomist His has also observed the phenomenon.[26] Seven years ago Boldireff demonstrated that the whole gastro-intestinal tract has a periodic activity while not digesting.[27] Each period of activity lasts from twenty to thirty minutes, and is characterized in the stomach by rhythmic contractions 10 to 20 in number. These contractions, Boldireff reports, may be stronger than during digestion, and his published records clearly support this statement. The intervals of repose between periodic recurrences of the contractions last from one and a half to two and a half hours. Especially noteworthy is Boldireff's observation that if fasting is continued for two or three days the groups of contractions appear at gradually longer intervals and last for gradually shorter periods, and thereupon the gastric glands begin continuous secretion, and all movements cease. All these testimonies to increased tone and periodic pulsations definitely prove, contrary to previous statements, that the empty stomach may be the seat of vigorous muscular activities.

Boldireff considered hunger in relation to the activities he described, but solely with the idea that hunger might *provoke* them; and since the activities dwindled in force and frequence as time passed, whereas in his belief they should have become more pronounced, he abandoned the notion of any relation between the phenomena.[28] Did not Boldireff misinterpret his own observations? When he was considering whether hunger might cause the contractions, did he not overlook the possibility that the contractions might cause hunger? A number of experiences have led to the conviction that Boldireff did, indeed, fail to perceive part of the significance of his results. For example, in auscultation of the alimentary canal relatively loud borborygmi have been noted as the hunger pangs were disappearing. Again the sensation

[24] Bettmann: Philadelphia monthly medical journal, 1899, 1, p. 133.

[25] Wolff: Dissertation, Giessen, 1902, p. 9.

[26] His: Archiv für Anatomie, 1903, p. 345.

[27] Boldireff: Archives biologiques de St. Petersburg, 1905, xi, p. 1. See also Ergebnisse der Physiologie, 1911, xi, p. 182.

[28] Boldireff: *Loc. cit.*, p. 96.

can be momentarily abolished a few seconds after swallowing a small accumulation of saliva or a tablespoonful of water. Since the stomach is in high tonus in hunger, this result can be accounted for as due to the momentary inhibition of the tonus by swallowing.[29] Thus also could be explained the disappearance of the ache soon after eating is begun, for repeated swallowing results in continued inhibition.

The concomitance of contractions and hunger in man. — Although the evidence above mentioned had led to the conviction that hunger results from contractions of the alimentary canal, direct proof was still lacking. In order to learn whether such proof might be secured, one of us (W.) determined to become accustomed to the presence of a rubber tube in the œsophagus.[30] Almost every day for several weeks W. introduced as far as the stomach a small tube, to the lower end of which was attached a soft-rubber balloon about 8 cm. in diameter. The tube was thus carried about each time for two or three hours. After this preliminary experience the introduction of the tube, and its presence in the gullet and stomach, were not at all disturbing. When a record was to be taken, the balloon, placed just below the cardia, was moderately distended with air, and was connected with a water manometer ending in a cylindrical chamber 3.5 cm. wide. A float recorder resting on the water in the chamber permitted registering any contractions of the fundus of the stomach. On the days of observation W. would abstain from breakfast, or eat sparingly, and without taking any luncheon would appear in the laboratory about two o'clock. The recording apparatus was arranged as above described. In order to avoid the possibility of an artifact, a pneumograph, fastened below the ribs, was made to record the movements of the abdominal wall. Between the records of gastric pressure and abdominal movement one electromagnetic signal marked time in minutes, and another traced a line which could be altered by pressing a key. All these recording arrangements were out of W's sight; he sat with one hand at the key, ready, whenever the sensation of hunger was experienced, to make the current which moved the signal.

When W. stated that he was hungry, powerful contractions of the

[29] Cannon and Lieb: this Journal, 1911, xxix, p. 267.

[30] Nicolai (*Loc. cit.*) reported that although the introduction of a stomach tube at first abolished hunger in his subjects, with repeated use the effects became insignificant.

stomach were invariably being registered. The record of W's introspection of his hunger pangs agreed closely with the record of his gastric contractions. Almost invariably, however, the contraction nearly reached its maximum before the record of the sensation was started (see Fig. 1). This fact may be regarded as evidence that the contraction precedes the sensation, and not *vice versa*, as Boldireff considered it. The contractions were about a half-minute in duration, and the intervals between varied from thirty to ninety seconds, with an average of about one minute. W's augmentations of intragastric pressure ranged between 11 and 13 in twenty minutes; C. had previously counted in himself 11 hunger pangs in the same time (see ten-minute record, p. 444). The rate in each of us, therefore, proved to be approximately the same. This rate is slightly slower than that found in dogs by Boldireff; the difference is perhaps correlated with the slower rhythm of gastric peristalsis in man compared with that in the dog.[31]

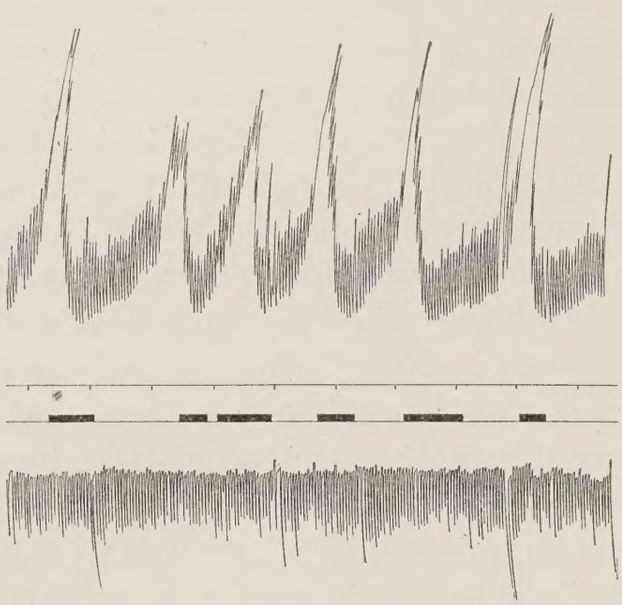


FIGURE 1. — One half the original size. The top record represents intragastric pressure (the small oscillations due to respiration, the large to contractions of the stomach); the second record is time in minutes (ten minutes); the third record is W's report of hunger pangs; the lowest record is respiration registered by means of a pneumograph about the abdomen.

Before hunger was experienced by W. the recording apparatus revealed no signs of gastric activity. Sometimes a rather tedious period of waiting had to be endured before contractions occurred, and after they began they continued for a while, then ceased (see Fig. 2). The feeling of hunger, which was reported while the contractions were recurring, disappeared when they stopped. The inability of the subject to control the contractions eliminated the possibility of their

[31] CANNON: The mechanical factors of digestion, London and New York, 1911, p. 54.

being artifacts, perhaps induced by suggestion. The close concomitance of the contractions with hunger pangs, therefore, clearly indicates that they are the real source of those pangs.

Boldireff's studies proved that when the empty stomach is manifesting periodic contractions the intestines also are active. Conceiv-

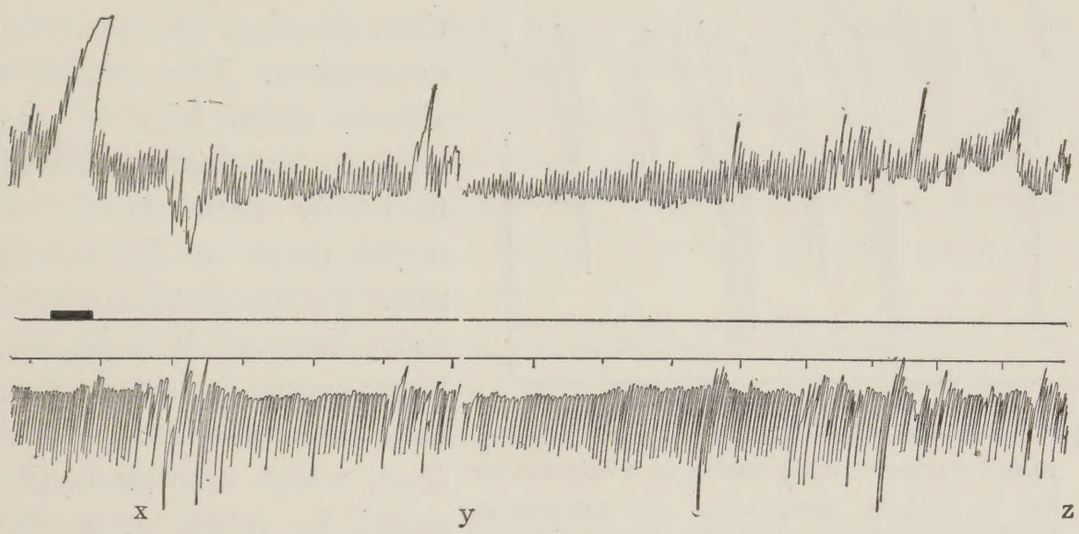


FIGURE 2. — One half the original size. The same conditions as in Fig. 1 (fifteen minutes). There was a long wait for hunger to disappear. After *x*, W. reported himself "tired, but not hungry." The record from *y* to *z* was the continuance, on a second drum, of *x* to *y*.

ably all parts of the alimentary canal composed of smooth muscle share in these movements. The lower œsophagus in man is provided with smooth muscle. It was possible to determine whether this region in W. was active during hunger.

To the œsophageal tube a thin-rubber finger cot (2 cm. in length) was attached and lowered into the stomach. The little rubber bag was distended with air, and the tube, pinched to keep the bag inflated, was gently withdrawn until resistance was felt. The air was now released from the bag, and the tube further withdrawn about 3 cm. The bag was again distended with air at a manometric pressure of 10 cm. of water. Inspiration now caused the writing lever, which recorded the pressure changes, to rise; and a slightly further withdrawal of the tube changed the rise, on inspiration, to a fall. The former position of the tube, therefore, was above the gastric cavity and below the diaphragm. In this position the bag, attached to a float recorder (with chamber 2.3 cm. in diameter) registered the periodic oscillations shown in Fig. 3. Though individually more prolonged than those of the stomach,

these contractions, it will be noted, occur at about the same rate. It is probable that the periodic activity of the two regions is simultaneous, for otherwise the stomach would force its gaseous content into the œsophagus with the rise of intragastric pressure.

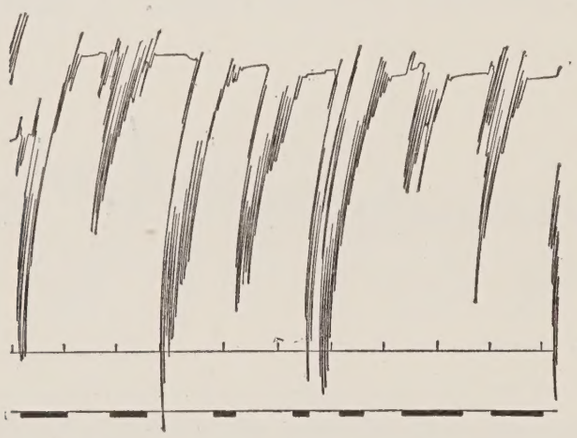


FIGURE 3. — One half the original size. The top record represents compression of a thin-rubber bag in the lower œsophagus. The pressure in the bag varied between 9 and 13 cm. of water. The cylinder of the recorder was of smaller diameter than that used in the gastric records. The œsophageal contractions compressed the bag so completely that, at the summits of the large oscillations, the respirations were not registered. When the oscillations dropped to the time line, the bag was about half inflated. The middle line registers time in minutes (ten minutes). The bottom record is W's report of hunger pangs.

What causes the contractions to occur has not been determined. From evidence already given they do not seem to be directly related to bodily need. Habit no doubt plays an important rôle. For present considerations, however, it is enough that they do occur, and that they are abolished when food, which satisfies bodily need, is taken into the stomach. By such indirection are performed some of the most fundamental of the bodily functions.

Peculiarities of hunger explained by contractions. — If these contractions are admitted as the cause of hunger, most of the difficulties confronting other explanations are readily obviated. Thus the occurrence of hunger at meal-times is most natural, for, as the regularity of defecation indicates, the alimentary canal has habits. Activity returns at the usual meal-time as the result of custom. By taking food regularly at a definite hour in the evening for several days, a new hunger period can be established. Since at these times the empty stomach, as Boldireff showed, has stronger contractions than the filled organ, hunger is aroused.

The contractions furthermore explain the sudden onset of hunger and its peculiar periodicity — phenomena which no other explanation of hunger can account for. The quick development of the sensation after taking a cold drink is possibly associated with the well-known power of cold to induce contraction in smooth muscle.

The great intensity of hunger during the first day of starvation, and its gradual disappearance till it vanishes on the third or fourth day, are made quite clear, for Boldireff observed that gastric contractions in his fasting dogs went through precisely such alterations of intensity and were not seen after the third day.

In fever, when bodily material is being most rapidly used, hunger is absent. Its absence is understood from an observation reported four years ago, that infection with systemic involvement is accompanied by a total cessation of all movements of the alimentary canal.[32] Boldireff observed that when his dogs were fatigued the rhythmic contractions failed to appear. Being "too tired to eat" is thereby given a rational explanation.

Another pathological form of the sensation — the inordinate hunger (bulimia) of certain neurotics — is in accord with the well-known disturbances of the tonic innervation of the alimentary canal in such individuals.

Since the lower end of the œsophagus, as well as the stomach, contracts periodically in hunger, the reference of the sensation to the sternum by the ignorant persons questioned by Schiff was wholly natural. The activity of the lower œsophagus also explains why, after the stomach has been removed, or in some cases when the stomach is distended with food, hunger can still be experienced. Conceivably the intestines also originate vague sensations by their contractions. Indeed the final banishment of the modified hunger sensation in the patient with duodenal fistula, described by Busch, may have been due to the lessened activity of the intestines when chyme was injected into them.

The observations recorded in this paper have, as already noted, numerous points of similarity to Boldireff's observations on the periodic activity of the alimentary canal in fasting dogs. Each period of activity, he found, comprised not only widespread contractions of the digestive canal, but also the pouring out of bile, and of pancreatic and intestinal juices rich in ferments. Gastric juice was not secreted at these times; when it was secreted and reached the intestine, the periodic activity ceased.[33] What is the significance of

[32] Cannon and Murphy: Journal of the American Medical Association, 1907, xlix, p. 840.

[33] Boldireff: *Loc. cit.*, pp. 108–111.

this extensive disturbance? Recently evidence has been presented that gastric peristalsis is dependent on the stretching of gastric muscle when tonically contracted.[34] The evidence that the stomach is in fact strongly contracted in hunger — *i. e.*, in a state of high tone — has been presented above.[35] Thus the very condition which causes hunger and leads to the taking of food is the condition, when the swallowed food stretches the shortened muscles, for immediate starting of gastric peristalsis. In this connection the recent observations of Haudek and Stigler are probably significant. They found that the stomach discharges its contents more rapidly if food is eaten in hunger than if not so eaten.[36] Hunger, in other words, is normally the signal that the stomach is contracted for action; the unpleasantness of hunger leads to eating; eating starts gastric secretion, distends the contracted organ, initiates the movements of gastric digestion, and abolishes the sensation. Meanwhile pancreatic and intestinal juices, as well as bile, have been prepared in the duodenum to receive the oncoming chyme. The periodic activity of the alimentary canal in fasting, therefore, is not solely the source of hunger pangs, but is at the same time an exhibition in the digestive organs of readiness for prompt attack on the food swallowed by the hungry animal.

[34] CANNON: this Journal, 1911, xxix, p. 250.

[35] The "empty" stomach and œsophagus contain gas (see HERTZ: Quarterly journal of medicine, 1910, iii, p. 378; MIKULICZ: Mittheilungen aus dem Grenzgebieten der Medicin und Chirurgie, 1903, xii, p. 596). They would naturally manifest rhythmic contractions on shortening tonically on their content.

[36] HAUDEK and STIGLER: Archiv für die gesammte Physiologie, 1910, cxxxiii, p. 159.

THE UNIVERSITY PRESS, CAMBRIDGE, U. S. A.